

Body size, age and sexual dimorphism in the genus *Salamandra*. A study of the Balkan species

(Amphibia, Urodela, Salamandridae)

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We studied two in many respect different Balkan salamander species (*Salamandra atra* and *S. salamandra*) in order to characterise their sexual size differences, as well as the age structure, correlations between age and morphometric traits, and survival rate of adult females and males. On the ground of morphometrics, in the samples of *S. salamandra* a number of statistically significant intersex differences was found between morphometric traits related with over-all size relations, feeding and locomotion abilities, with a marked population effect. However, genders of *S. atra* were much more alike. In both species, female-male differences in life span and timing of sexual maturity appeared to be negligible, while females had non-significantly higher mortality rate than males.

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Introduction

The importance of body size in ecology, life history, and reproductive fitness has been widely acknowledged for years (e.g. Fairbairn 1997). Thus, the patterns of interspecific variation in body size are expected to reflect patterns of adaptive divergence, which is true not only for the mean size of the species, but also for the sizes of each sex.

It is a commonplace in batrachology that females grow larger than males in most taxa, i.e. these taxa exhibit female-biased sexual size dimorphism (hereafter abbreviated to SSD) (e.g. Shine 1979, Duellman & Trueb 1986, Halliday & Tejedo 1995). However, many amphibian groups still remain to be explored in this respect more carefully. The European salamanders of the genus *Salamandra*, especially the two species inhabiting the Balkan Peninsula: the fire salamander (*Salamandra salamandra*) and the alpine salamander (*Salamandra atra*) are among them. Highly polytypic *S. salamandra* is the most widely distributed species among the fire salamanders species group (*S. salamandra*, *S. corsica*, *S. algira* and *S. infraimmaculata*). It has a mostly west Palaearctic distribution: from southwest France, through central Europe and the Balkan Peninsula to the Black Sea (see Klewen 1991, Veith 1994, Griffiths 1996). The range of the alpine salamander is much smaller (the Alps and the Dinaridian mountains), and so far only three subspecies have been described. These two salamander species appeared to be different in many other respects. The alpine salamander can be found only in cool and damp mountainous localities, in the Balkan at an altitude above 1.500 m a.s.l, mostly above the tree line. On the contrary, the fire salamander is encountered in much more mesophilic climate providing shade and moisture.

It cannot be found above 1.700 m in the Balkan. Also, profound differences occur in the mode of reproduction. Embryonic development and metamorphosis are completed in oviducts of *S. atra*. The fire salamanders have variable reproductive modes; its eggs hatch prior to, or simultaneously with parturition. The young are mostly born as gill-bearing larvae, which after a period of aquatic existence metamorphose into juvenile form and leave water to continue their life on land.

It is widely accepted that males of the fire salamander are somewhat smaller than females (Degani 1986, Rebelo & Caetano 1995, Klewen 1986), with a slender body and longer limbs relative to body length (Eiselt 1958). Particularly during the breeding season, males have a more swollen cloaca than females. More scanty data on the sex body sizes in the alpine salamander indicate negligible difference. However, to the best of our knowledge, in depth sex-dimorphism study, especially allometry analysis conducted to reveal difference in their body shape, has never been done. Also, although the fire salamander is a well known and widespread tailed amphibian in Europe, age data obtained by skeletochronology have been so far scarcely known (see Warburg 1992, 1994, Rebelo & Caetano 1995), while data for the alpine salamander are only anecdotal ones (Fachbach 1988).

The aim of this paper was to study proximate aspects of SSD (i.e. direction, pattern and magnitude of sexual dimorphism) of the two Balkan salamander species, including the study of age structure parameters and the relations between age and morphometric characters.

Materials and methods

Materials

The adult alpine salamanders came from Slovenia (Mt. Kranjski Snežnik: 3♀♀, 6♂♂), and from Mt. Prokletije Massif (Lumbarška planina, Bogičevica, Djerovica; Serbia and Montenegro: 10♀♀). These samples belong to presumably different subspecies, *S. atra atra* and *S. a. prenjensis*, respectively (Džukić 1993). It is also of interest that the alpine salamander populations from Mt. Prokletije are the fringe ones (Krizmanić 1997). Adult fire salamanders were collected from the fields of two Serbian areas: Mt. Vršачki breg (Pojilo, Mesički potok: 6♀♀, 32♂♂), and on the hills near the town Despotovac (the river Resava valley; 14♀♀, 5♂♂). Adulthood of each specimen studied was confirmed by the inspection of gonads. Salamanders studied, except loaned ones, were deposited in the Georg Džukić's batrachological collection (Institute for Biological Research, Belgrade).

Morphometrics

The following sixteen morphometric characteristics were measured with digital calliper (to the nearest 0.01 mm) for each individual: L – total length, Lsv – snout-vent length (from the snout to the posterior edge of the cloaca basis), Lcd – tail length (from the anterior edge of the cloaca basis to the tail tip), Lc – head length (measured from the snout to the gular fold), Ltc – maximal head width (between mouth corners), Ac – maximal head height, D – distance between fore and hind limbs (axilla to groin), Lpa – forelimb length, Lpp – hindlimb length, Dn – internarial distance, Do – eye diameter, Spp – minimum interorbital distance, Lpr – parotoid gland length, A – manus length (from inner border of wrist to tip of third toe), P – pes length (from inner border of foot to tip of the forth toe), Lm – jaw length (measured from the snout to the corner of the mouth). The paired measurements were taken on the right side only, neglecting thus potential asymmetry. All data were log – transformed in order to normalise variables.

The nested ANOVA was used to reveal effects of sample and effects of sex (nested within sample) on morphometric variability in analysed salamander species. The t-tests were used to analyse differences in body weight and in morphometric traits between sexes. As measure of overall differences between sexes, the multivariate Mahalanobis' distance was calculated using all analysed morphometric traits.

The coefficients of bivariate allometry were estimated as regression coefficients from linear regression of logarithmically transformed morphometric data, using a snout-vent length as an independent size variable.

Age study

Ages of each individual were assessed by skeletochronology. A general description of this histological method can be found elsewhere (e.g. Castanet & Smirina 1990, Castanet et al. 1993). Sections of the diaphysis of toe phalanges were used to count the lines of arrested growth. Frozen sections of the demineralized bones were cut at 16 micrometers and stained in Ehrlich's hematoxylin. We managed to assess an individual onset of sexual maturity as a sudden decrease in bone growth and concomitant rapprochement of lines of arrested growth (see Kleinenberg & Smirina 1969, Francillon-Vieillot et al. 1990).

The differences in age of sexual maturity between sexes were analysed by nonparametric Wilcoxon two sample tests and by Kolmogorov-Smirnov tests for analysis of frequency distributions. The mean survival rate was roughly estimated from the age structure of analysed groups (Krebs 1989):

$SR = T / (N + T - 1)$, where T is the sum of the coded ages times their frequencies and N is the number of animals in x age class. The 95 % confidence intervals (CI) for survival rates were calculated as:

$CI = 1.96(pq - 1)^{1/2}$, where $q = (1 - p)$; and p is the survival rate and n is the simple size.

Results

Morphometrics

In the alpine salamander statistically significant differences among populations were found for four of 16 morphometric traits (Tab. 1). Also, there were no differences in morphometric variability between genders of this salamander. To ensure a sufficient number of individuals of each sex for further analyses, we pooled specimens of alpine newt from different localities into one sample. The mean values (\pm SE) and ranges of body weight and 16 morphometric traits of the alpine salamander samples are given in Tab. 2.

The differences between samples of *S. salamandra* were much more pronounced. The samples significantly differed in variability of all traits, except for the interorbital distance. The sex factor influenced variability of body weight, head width, and traits closely related with locomotion (lengths of forelimb and tail) (Tab. 1). Individuals from the Despotovac population sample had somewhat larger dimensions of all analysed traits comparing with those from the Vršac population (Tabs 3 and 4).

The alpine salamander females appeared to be slightly larger than males for the most characters measured, but only females interorbital distances were significantly larger than in males ($t=2.56$; $df=17$; $P<0.05$). The differences between sexes were much more pronounced in the fire salamander. In the population sample from Despotovac males were significantly larger than females for the body length ($t=2.37$; $df=17$; $P<0.05$), as well as for forelimb ($t=3.61$; $df=17$; $P<0.01$), manus ($t=2.82$; $df=17$; $P<0.05$), and tail length ($t=2.83$; $df=17$; $P<0.05$). In the population sample from Vršac, females were significantly heavier ($t=4.35$; $df=36$; $P<0.001$), with wider head ($t=2.63$; $df=36$; $P<0.05$) and larger parotoid glands than males ($t=2.13$; $df=36$; $P<0.05$). On the contrary, males had slightly larger forelimbs, manus, peas and tail length than females, but these differences were statistically nonsignificant.

The Mahalanobis' distance analysis also showed that there was no significant difference between the alpine salamander females and males ($D^2=15.41$, $F_{(Ndf=16; Ddf=2)}=0.46$, $P>0.851$). The overall differences between genders of the fire salamander varied geographically. In the Despotovac population sample the overall difference between sexes was insignificant ($D^2=31.1$, $F_{(Ndf=16; Ddf=2)}=0.84$, $P>0.05$), while in the Vršac population sample this difference appeared to be highly statistically significant ($D^2=25.43$, $F_{(Ndf=16; Ddf=21)}=4.68$, $P<0.01$).

Bivariate allometry

In the alpine salamander most of analysed traits showed an isometric growth. A statistically significant positive bipartite allometry was found only for the head length ($b=1.234 \pm 0.387$; $P<0.05$), the distance between nostrils in females

($b=0.491 \pm 0.669$; $P<0.05$), and for the total body length in males ($b=1.248 \pm 0.062$; $P<0.05$), while the distance between orbits in males showed a negative allometric growth ($b=-0.818 \pm 0.391$; $P<0.01$). In the fire salamander from the Despotovac population sample the statistically significant positive

Table 1. The differences between populations and between females and males in body weight and 16 morphometric traits in *Salamandra atra* and *Salamandra salamandra*. F values are obtained from nested ANOVA, with sex factor nested within population factor. For character symbols see text.

	<i>S. atra</i> (n=19)				<i>S. salamandra</i> (n=57)			
	Population (df=1)		Sex (df=1)		Population (df=1)		Sex (df=1)	
	F	P	F	P	F	P	F	P
W	/	/	/	/	30.49	0.0001	11.24	0.001
L	0.52	0.480	0.45	0.5097	18.97	0.0001	2.11	0.1309
Lsv	1.59	0.2247	0.56	0.4669	27.60	0.0001	0.78	0.4622
Lc	4.76	0.0443	2.43	0.1390	10.89	0.0017	0.28	0.7587
Lcd	0.20	0.6633	0.38	0.5437	6.11	0.0167	6.36	0.0033
Ltc	1.74	0.2063	0.30	0.5935	33.04	0.0001	3.58	0.0347
Ac	3.97	0.0637	0.19	0.6722	23.87	0.0001	1.58	0.2148
D	0.01	0.9761	0.05	0.8343	13.94	0.0005	1.18	0.3154
Lpa	0.50	0.4882	0.42	0.5278	17.03	0.0001	6.22	0.0038
Lpp	2.41	0.1405	0.72	0.4077	10.08	0.0025	1.37	0.2642
Dn	0.19	0.6652	0.27	0.6127	16.50	0.0002	0.63	0.5381
Do	4.20	0.0572	0.10	0.7613	15.11	0.0003	1.16	0.3222
Spp	9.31	0.0076	0.32	0.5821	1.79	0.1864	1.13	0.3315
Lpr	4.76	0.0444	0.23	0.6392	4.40	0.0407	2.13	0.1294
A	0.10	0.7510	0.08	0.7840	4.63	0.0359	2.17	0.1242
P	0.25	0.6261	0.01	0.9376	8.73	0.0047	1.98	0.1486
Lm	4.90	0.0312	1.06	0.3542	4.90	0.0312	1.06	0.3542

Table 2. Mean values, standard errors and ranges of body weight (in gr) and 16 morphometric traits (in mm) of *Salamandra atra* females and males. For character symbols see text.

	Females (n=13)		Males (n=6)	
	Mean ± SE	Range	Mean ± SE	Range
W	8.70±0.44	6.5-10.0	/ ± /	/ - /
L	114.0±2.72	96.7-126.2	114.44±4.53	93.2-123.8
Lsv	67.94±1.45	59.5-74.4	16.31±0.74	56.9-73.2
Lc	16.60±0.63	12.9-20.1	16.31±0.74	13.5-18.2
Lcd	50.99±1.78	41.4-59.4	51.71±2.66	40.0-58.8
Ltc	12.63±0.35	10.5-14.8	12.28±0.41	11.1-13.7
Ac	7.25±0.55	4.7-10.2	6.25±0.40	5.8-7.8
D	33.97±1.10	27.6-40.1	34.24±1.43	27.8-38.2
Lpa	19.74±0.67	16.5-23.6	19.72±1.22	15.5-23.6
Lpp	21.33±0.84	17.6-26.3	20.74±1.11	16.9-24.1
Dn	4.36±0.21	3.0-5.5	4.36±0.17	3.8-5.0
Do	3.26±0.27	2.2-5.0	3.65±0.15	3.1-4.0
Spp	5.03±0.37	3.8-7.7	3.75±0.15	3.4-4.4
Lpr	8.99±0.32	6.8-10.5	8.35±0.43	7.3-9.8
A	7.44±0.28	6.1-9.1	7.20±0.48	5.9-9.1
P	9.53±0.46	6.3-12.7	9.80±0.77	8.3-12.3
Lm	10.02±0.23	8.7-11.4	10.36±0.49	8.3-11.9

allometry was found for the head width in females ($b = 0.58 \pm 0.25$; $P < 0.05$) and the manus length in males ($b = 0.109 \pm 0.199$; $P < 0.05$). The length of parotoid gland and tail length in females from this population showed the statistically significant negative allometry ($b = -0.076 \pm 0.373$; $P < 0.05$ and $b = -0.503 \pm 0.504$; $P < 0.05$, respectively). In the fire salamander from the Vršac population sample, the

Table 3. Mean values, standard errors and ranges of body weight (in gr) and 16 morphometric traits (in mm) of *Salamandra salamandra* females and males from population Despotovac. For character symbols see text.

	Females (n=14)		Males (n=5)	
	Mean ± SE	Range	Mean ± SE	Range
W	48.78±2.177	36.94-67.28	50.21±2.18	45.79-56.53
L	182.38±3.52	154.51-99.8	197.57±2.88	189.71-207.37
Lsv	116.86±1.63	109.1-127.3	119.83±2.00	112.41-124.46
Lc	25.84±0.45	22.5-28.6	26.42±0.52	24.44-27.44
Lcd	73.10±2.50	52.0-84.8	86.77±1.71	84.25-93.50
Ltc	21.56±0.32	19.8-23.7	21.56±0.82	19.40-23.78
Ac	14.78±0.34	13.2-17.2	15.13±0.41	14.10-16.34
D	63.62±1.38	54.6-73.2	62.52±2.33	53.60-66.72
Lpa	35.02±0.75	29.1-38.9	40.12±0.59	38.62-41.74
Lpp	37.17±0.70	33.1-41.0	39.70±0.74	37.81-42.30
Dn	7.79±0.18	6.8-8.9	7.85±0.20	7.26-8.43
Do	5.99±0.17	4.7-6.8	6.57±0.20	5.96-7.03
Spp	6.72±0.22	5.2-8.0	6.26±0.14	5.72-6.47
Lpr	13.53±0.37	11.5-15.8	13.30±0.75	10.8-14.59
A	12.73±0.20	11.8-14.5	13.80±0.30	13.33-14.90
P	15.22±0.30	13.5-17.0	16.32±0.41	14.81-17.30
Lm	16.80±0.30	14.8-18.6	17.85±0.54	16.8-19.70

Table 4. Mean values, standard errors and ranges of body weight (in gr) and 16 morphometric traits (in mm) of *Salamandra salamandra* females and males from population Vršac. For character symbols see text.

	Females (n=6)		Males (n=32)	
	Mean ± SE	Range	Mean ± SE	Range
W	41.76±2.39	34.73-50.11	27.81±1.09	16.88-40.66
L	168.62±0.89	166.62-172.68	170.08±2.63	142.68-199.56
Lsv	105.51±2.48	100.42-116.38	102.16±1.56	86.60-119.86
Lc	23.98±0.35	22.99-25.46	23.62±0.41	19.40-28.78
Lcd	70.01±2.86	60.68-77.41	75.54±1.34	61.48-92.80
Ltc	19.67±0.36	18.59-20.62	18.21±0.23	15.78-21.02
Ac	12.54±0.49	10.62-14.13	11.37±0.33	8.12-15.40
D	57.66±1.65	51.40-62.55	54.33±0.96	43.65-63.38
Lpa	32.25±0.94	28.59-35.47	34.36±0.55	26.86-40.30
Lpp	35.42±0.69	32.64-37.26	34.99±0.58	29.32-42.09
Dn	6.815±0.27	5.59-7.60	7.10±0.11	5.91-8.60
Do	5.28±0.23	4.64-6.20	5.39±0.12	3.42-6.64
Spp	6.31±0.22	5.79-7.07	5.91±0.17	4.10-8.61
Lpr	13.05±0.57	10.46-14.44	11.92±0.18	9.16-13.69
A	11.50±0.82	8.75-13.41	12.77±0.34	8.17-16.35
P	13.82±0.40	12.28-14.84	14.778±0.30	11.88-19.27
Lm	16.33±0.50	15.43-18.73	15.648±0.35	10.80-19.92

positive allometric growth was found for the hindlimb ($b=0.260 \pm 0.250$; $P<0.05$) and manus lengths ($b=0.249 \pm 0.254$; $P<0.05$) in females, and the head width ($b=0.708 \pm 0.072$; $P<0.001$), internarial distance ($b=0.714 \pm 0.126$; $P<0.05$) and length of parotoid gland in males ($b=0.656 \pm 0.151$; $P<0.05$). In females from this population the statistically significant negative allometric growth was also found for the tail length ($b=-1.330 \pm 0.631$; $P<0.05$) and for the interorbital distance ($b=-0.615 \pm 0.292$; $P<0.01$).

Wolterstorff index

The measures of interlimb distance and the length of the fore-limb, combined in a Wolterstorff's index (WI, see Arntzen & Wallis 1994) show sexual dimorphism in some European tailed amphibians, especially of the crested newt species (*Triturus cristatus* superspecies), including the fire salamander (Eiselt 1958). The values of this index are usually higher in males than in females. In the fire salamander sample from Despotovac population sample WI values ranged from 0.460 to 0.662 for females (mean \pm SE=0.554 \pm 0.016), and for males from 0.579 to 0.726, (mean \pm SE=0.645 \pm 0.025). Intersex difference appeared to be statistically significant ($t=3.1$, $P<0.05$). The main value of WI in the population sample from Vršac was 0.561 \pm 0.017 (range 0.505-0.611) for females and 0.635 \pm 0.008 (range 0.529-0.760) for males. The intersex difference was also statistically significant ($t=3.813$, $P<0.01$). Thus, males of the fire salamander from the Balkans were more limb-lengthed relative to the interlimb distance. This indicates their greater locomotory efficiency which has been proved by their greater activity compared to females during the breeding season (see Warburg 1994). However, there was no such difference between genders of the alpine salamander ($t=0.218$, $P>0.05$). The mean WI value for females was 0.584 \pm 0.016 (range 0.488-0.704), and for males 0.577 \pm 0.028 (range 0.492-0.668).

Age structure and time of sexual maturity

As the population effect for longevity and time of sexual maturity appeared to be negligible in both species, samples were pooled for statistical analyses. We estimated that all the adult specimens examined were at least in their fifth year of posthatching life. The oldest male among the fire salamanders was 13 years old, and the oldest female was 14 years old, with the average age of 7.91 \pm 0.47 for males, and 8.20 \pm 0.44 for females. In the alpine salamanders these figures were lower; 10 years was the age of the oldest male and 11 years of the oldest female, with the mean age of 7.00 \pm 0.86 and 7.08 \pm 0.54, respectively. No significant differences were found between the age distributions of the two genders in either species (Wilcoxon two sample test, $P>0.05$), (Figs 1 and 2). Also, there were no statistically significant differences in frequency distributions of age classes between females and males in both species (Kolmogorov-Smirnov test, $P>0.05$).

On the average, the attainment of sexual maturity was somewhat prolonged in females compared to males in the alpine salamander (3.20 \pm 0.29 vs. 2.25 \pm 0.25, with the range of 2-4 and 2-3 yrs. for females and males, respectively). However, the average time of sexual maturity in the fire salamander was somewhat higher in males (3.40 \pm 0.18, range 2-5 yrs.) than in females (3.00 \pm 0.15, range 2-5). Nevertheless, intersex difference for this life-history trait appeared to be statistically non-significant in both species (Wilcoxon two sample test, $P>0.05$).

Survival Rate

In the alpine salamander the roughly estimated survival rate ranged from 0.526 (CI=0.295) for females to 0.615 (CI=0.295) in males. In other words, on the average 53 % of female and 61 % of male individuals survive from one year to the other. In the fire salamander the estimated survival rates ranged from 0.536 (CI=0.224) in females to 0.787 (CI=0.144) in males. These results indicated that females had higher mortality than males in both species, but as confidence intervals overlapped, these differences were non-significant.

Correlations between size measures and age and time of sexual maturity

The time of attainment of sexual maturity had no significant correlation with any body size measures, regardless of sex, in both analysed species, as was the case with age in the alpine salamander. In the fire salamander the statistically significant correlation between body size and age was found only in males from the Vršac population sample. In this group majority of analysed traits were correlated with age. These include: body weight, body and tail lengths and snout-vent length, head measures, forelimb length, hindlimb lengths, the size of parotoid gland and internarial distance (significancy at least $P<0.05$).

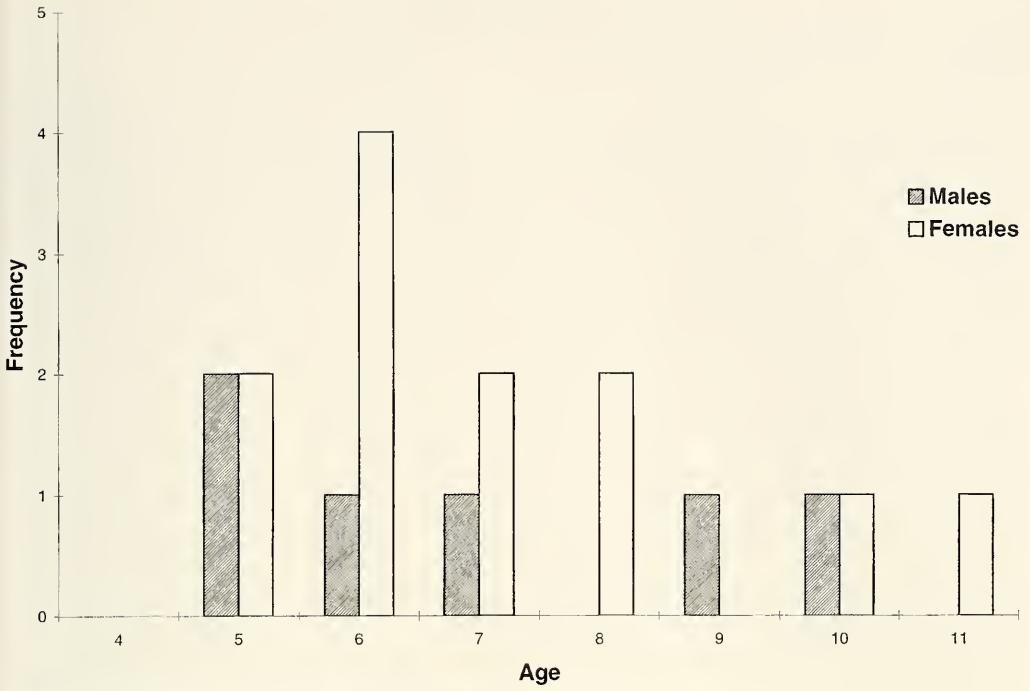


Fig. 1. Age distribution for males and females of *Salamandra atra*.

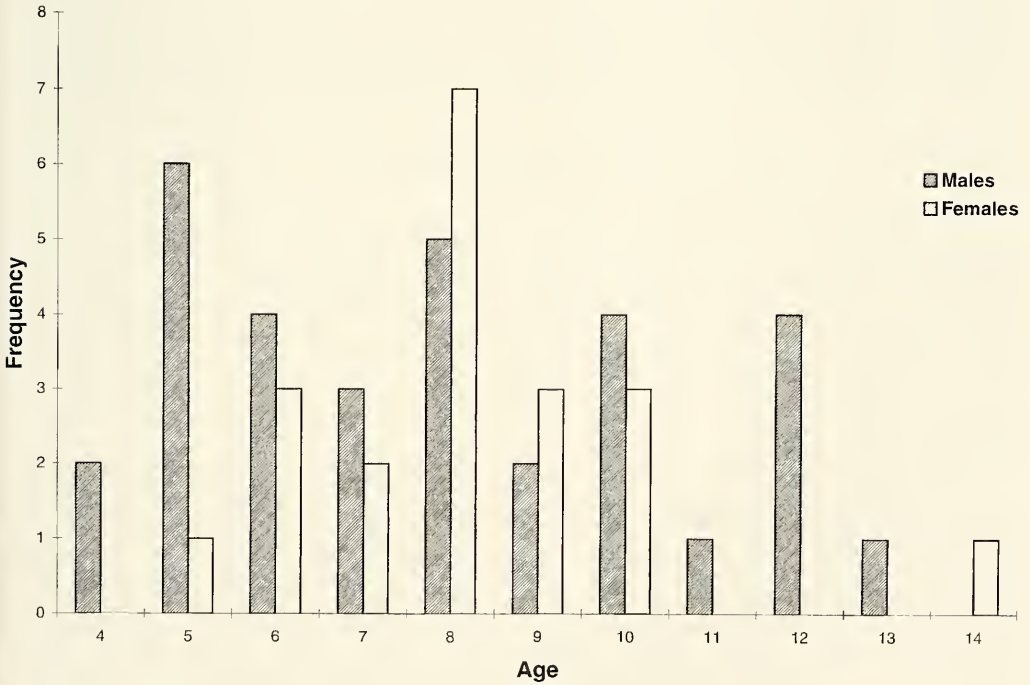


Fig. 2. Age distribution for males and females of *Salamandra salamandra*.

Body size and age

The body size of the fire salamander we studied is well within the range for these species so far recorded for the Balkan Peninsula. Thus, Džukić (1993) stated that the mean value of the total body length for the sexually matured fire salamanders from Serbia was 181 ± 18 mm ($N=170$), with the highest value of 245 mm (♀ from Novo Brdo, Zebince, Kosovo). Similar values were found for other Balkan populations studied (Bulgaria, Bureš & Cončev 1963; Roumania, Fuhn 1960; Hungary, Dely 1966). For the alpine salamander an appreciable number of specimens measured came from the Prenj and Cvrstica mountains (Bosnia and Hercegovina) and those specimens appeared to be somewhat larger (Klewen 1991) in comparison to individuals we studied. Specimens from Balkan, both females and males, were on average larger than those from different localities of the Italian and Switzerland part of Alps (Nasceti et al. 1988) but the differences were not significant (t-test, $P>0.05$).

In general, there is a trend to increased longevity, and to less extent, an age of maturation in northern and mountain amphibian populations as compared to southern and lowland populations (e.g. Smirina 1994). It was found that a long phase of hibernation, followed by a comparatively short period of activity at a high altitude of the Alps in Austria, led to considerably delayed sexual maturity and increased longevity for the alpine newt (*Triturus alpestris*; Schabetsberger & Goldschmid 1994) in comparison with Balkan populations (Smirina & Sofianidou 1985, Kalezić et al. 1996). However, such relationships between these life-history characteristics and the altitude of the breeding site seem not to hold for the alpine salamander in comparison to the fire salamander that inhabits temperate environment. But, our alpine salamanders were much younger than those from the Austrian Alps (longevity maximum after metamorphosis 14-15 yrs., age of sexual maturation 4-5 yrs.; Fachbach 1988). In contrast to the above hypothesis is the fact that fire salamanders from the Balkan Peninsula appeared to be younger than those from Portugal (18-19 years, Rebelo & Caetano 1995) and from Israel (20 years, Warburg 1994).

Among life history characteristics the timing of maturation is a critical event influencing the morphology and fitness (i.e. lifetime reproductive success) of individuals, as well as the demographic structure of populations and species (Stearns 1991, Roff 1992). This trait seems to be rather conservative in the genus *Salamandra*, regardless of the region studied, ranging from 2-4 yrs. for females and 2-5 yrs for males (this study), or 3-4 yrs. vs. 2-3 yrs. (Rebelo & Caetano 1995). In numerous amphibian species females delay the age of sexual maturation by one to three years later than males (Halliday & Tejedo 1995). By delaying maturation, females attain larger body-size at first breeding with a resulting benefit in reproductive performance. In *Salamandra* species this apparently varies according to the region studied – this generality holds for the Portugal fire salamander (Rebelo & Caetano 1995), but fails for the Balkan salamanders (this study).

Sexual dimorphism

There is a large array of factors that affect sexual size dimorphism. In general, sexual size dimorphism of any species may be a consequence of differences in some life-history traits and sex-related action of sexual and/or natural selection, including fecundity selection. Thus, the direction and the degree of SSD are the result of different selective regimes usually acting separately on females and males. The importance of these regimes varies among species and populations, or even with time in the same population.

It was claimed that in amphibians selection on female body size was, contrary to that on the male body size, "typically more uniform in direction and intensity because of the strong correlation between body-size and measures of reproductive success such as fecundity and offspring size" (Halliday & Tejedo 1995, p. 438). Also, for amphibians in general, selection for higher fecundity in females causes their larger body size than in males (Halliday & Tejedo 1995). In the alpine salamander, a rare species among tailed amphibians with viviparous reproduction (Wake 1993), a female, regardless of body size, gives birth to only one or usually two fully metamorphosed youngs. The offspring, during the first year of lengthy oviductal gestation (2-5 years), feed on remaining yolked eggs of an initial clutch numbered 20-30 eggs per ovary (Griffiths 1995). In the case of slight variation of reproductive output, fecundity selection could be at least released. If there is neither pronounced selection for larger male body size,

nor differences in life-history traits, no sexual size dimorphism may be the outcome. It seems that the absence of genders size and shape differences is the characteristic of other alpine salamander populations (i.e. from Italy and Switzerland), and the same holds for the close species of the black salamander *S. lanzai* (Nasceti et al. 1988).

The fire salamander, however, harbours intersex differences in many measures expressing over-all size relations, locomotion abilities, as well as in body shape parameters. In many parts of the species range: e.g. Israel (Degani 1986), Portugal (Rebelo & Caetano 1995), Germany (Klewen 1986) females were somewhat bigger than males, significantly or not, while in the Balkans a reverse trend was observed. Apparently, a direction and magnitude of SSD in the fire salamander is not consistent between areas studied and/or populations. This species is among urodeles in which fighting between males has been noticed (Kastle 1986). According to the predictions of sexual selection theory, males could be bigger than females (Halliday & Verrell 1986). On the other hand, due to highly variable females reproductive output (clutch size can vary from 10 to 50 larvae) appreciable fecundity selection could be expected as well. What is about life-history traits that might influence the SSD in the fire salamander? Up to now it is known that intersex differences in the fire salamander life span and time of sexual maturity appeared to be statistically significantly different in the Portugal specimens (Rebelo & Caetano 1995). According to their study, males live longer than females, and tend to mature one year earlier than females. However, we found no evidence that males had a longer life-span than females, which also goes for the fire salamander from Israel (Warburg 1994). Also, there is no difference in the time of sexual attainment in the Balkan fire salamanders. Another life-history dimorphic trait that is potentially different between genders is the survival rate that is higher in males in comparison to females but without statistical significance. It might be speculated that SSD, observed in the fire salamander, is a correlated response to the differential growth rate of the two sexes during a juvenile phase that is the major period of growth during life span. This happens for example, in the crested alpine newt (*Triturus carnifex*; Cvetković et al. 1997, Kalezić & Djorović 1998).

The available samples of the Balkan salamander species were small and largely sex biased. A factors influencing the estimation of SSD could be a potential sample bias, especially when distributions of body-size and age may change in time even within populations (Halliday & Tejedo 1995) and potential measurement errors. Having lacked additional samples, geographical variation in the direction, pattern and magnitude of the sexual dimorphism were still far from fully explored matter. Apparently, much more research is needed to enlighten sexual size dimorphism in Salamandrida species as the first, and than, as a more difficult task, to resolve factors contributing to this dimorphism.

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References

- Arntzen, J. W. & G. P. Wallis 1994. The "Wolterstorff index" and its value to the taxonomy of the crested newt superspecies. – *Abh. Ber. Natur. Magdeburg* 17: 57-66
- Bookstein, F., B. Chernoff, R. Elder, J. Humphries, G. Smith & R. Stauss 1985. Morphometrics in Evolutionary Biology. – *Acad. Nat. Sciences, Philadelphia, Pennsylvania*
- Bureš, I. & J. Cončev 1963. Der Feuersalamander (*Salamandra salamandra* L.) im Vitosa-Gebirge. – *Bull. Inst. Zool. Muse* 13: 79-91 (In Bulgarian with German summary)
- Castanet, J. & E. Smirina 1990. Introduction to the skeletochronological method in amphibians and reptiles. – *Annls. Sci. Nat. Zool., Paris* 11: 191-196
- , H. Francillon-Vieillot, F.J. Meunier & A. De Ricqlès 1993. Bone and individual aging. – In: Bone. B. K. Hall (ed.), Vol. 7: pp. 245-283. CRC Press, Boca Raton, Florida
- Cvetković, D., M. L. Kalezić & G. Džukić 1997. Sexual size and shape difference in the crested newt (*Triturus carnifex*): Ontogenetic growth aspects. – *Alytes* 15: 37-48

- Degani, G. 1986. Plasma proteins and morphology of *Salamandra salamandra* in Israel. – *Amphibia-Reptilia* 7: 105-114
- Dely, G. O. 1966. Angaben über die Verbreitung des Feuersalamanders (*Salamandra salamandra*) im Karpatenbecken. – *Vertebrata Hungarica* 8: 69-88
- Duellman, W. E. & L. Trueb 1986. *Biology of Amphibians*. – MacGraw Hill, New York
- Džukić, G. 1993. Tailed Amphibians (Caudata) of Serbia: A Faunistical and Zoogeographical Study, Regarding Protection and Conservation. – Ph. D. Thesis, University of Belgrade (In Serbian with English summary)
- Eiselt, J. 1958. Der Feuersalamander *Salamandra salamandra* (L.), Beiträge zu einer taxonomischen Synthese. – *Abh. Ber. Natur. Vorgesch. Magdeburg* 10: 77-155
- Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. – *Ann. Rev. Ecol. Evolution* 28: 659-687
- Fachbach, G. 1988. Röhrenknochenentwicklung und Altersbestimmung bei *Salamandra atra* Laur., 1768 (Urodela, Salamandridae). – *Zool. Anz.* 221: 188-200
- Francillon-Vieillot, H., J. W. Arntzen & J. Geraude 1990. Age, growth and longevity of sympatric *Triturus cristatus*, *T. marmoratus* and their hybrids (Amphibia, Urodela): A skeletochronological comparisons. – *J. Herpetol.* 24: 13-22
- Fuhn, I. 1960. Fauna RP Romine. Amphibia. XIV (1). – *Acad. RP Romine, Bucuresti*
- Griffiths, R. A. 1996. *Newts and Salamanders of Europe*. – T & AD Poyser Natural History, London
- Halliday, T. R. & P. A. Verrell 1986. Sexual selection and body size in amphibians. – *Herpetol. J.* 1: 86-92
- Halliday, T. & M. Tejedo 1995. Intrasexual selection and alternative mating behaviour. In: *Amphibian Biology*, Vol. 2, Social Behaviour. H. Heatwole & B. K. Sullivan (eds.), pp. 419-468. – Surrey Beatty & Sons, Chipping Norton, NSW
- Kalezić, M. L., D. Cvetković, A. Djorović & G. Džukić 1996. Alternative life-history pathways: paedomorphosis and adult fitness in European newts (*Triturus vulgaris* and *T. alpestris*). – *J. Zool. Syst. Evol. Research* 33: 1-7
- & A. Djorović 1998. Life history dependent sexual size dimorphism in the crested newt (*Triturus cristatus*, Caudata). – *Folia-Zoologica* 47: 317-319
- Kastle, W. 1986. Rival combats in *Salamandra salamandra*. – In: *studies in Herpetology*. Z. Röcek (ed.), pp. 525-528. Prague
- Kleinberg, S. E. & E. M. Smirna. 1969. A contribution to the method age determination in amphibians. – *Zool. Zh.* 48: 1090-1094
- Klewen, R. 1986. Population ecology of *Salamandra salamandra terrestris* in an isolated habitat. – In: *Studies in Herpetology*. Z. Röcek (ed.), pp. 395-398. Prague
- 1991. Die Landsalamander Europas. Teil 1. – *Die Neue Brehm-Bücherei* 584, 2. ed., Ziemsen-Verlag, Lutherstadt-Wittenberg
- Krebs, C. J., 1989. *Ecological Methodology*. – Harper & Row Publishers, New York
- Krizmanić, I. 1997. New discovery of the species *Salamandra atra* (Laurenti, 1768; Salamandridae: Caudata) in the area of Prokletije. – *Univ. Thought Pristina* 3: 57-59
- Nascetti, G., F. Andreone, M. Capula & L. Bullini 1988. A new *salamandra* species from southwestern Alps (Amphibia, Urodela, Salamandridae). – *Boll. Mus. reg. Sci. nat. Torino* 6: 617-638
- Rebelo, R. & M. H. Caetano 1995. Use of the skeletochronological method for ecodemographical studies on *Salamandra salamandra gallica* from Portugal. – In: Lorente et al. (eds.): *Scientia Herpetologica*, pp. 135-140
- Roff, D. A. 1992. *The Evolution of Life Histories: Theory and Analysis*. – Chapman & Hall, New York
- Schabetsberger, R. & A. Goldschmid 1994. Age structure and survival rate in alpine newt (*Triturus alpestris*) at high altitude. – *Alytes* 12: 41-47
- Shine, R. 1979. Sexual selection and sexual dimorphism in the Amphibia. *Copeia* 1979: 297-306
- Smirina, E.M. 1994. Age determination and longevity in amphibians. – *Gerontology* 40: 133-146
- & T. Sofianidou 1985. On life span of the neotenic and metamorphosed alpine newts (*Triturus alpestris*) from high mountains of Greece. – *Zool. Zhur.* 64: 311-315 (In Russian with English Summary)
- Stearns, S. C. 1991. *The Evolution of Life Histories*. – Oxford University Press, New York
- Veith, M. 1994. Morphological, molecular and life-history variation in *Salamandra salamandra* (L.). – *Mertensiella* 4: 355-397
- Wake, M. H. 1993. Evolution of oviductal gestation in Amphibians. – *J. Exp. Zool.* 266: 394-413
- Warburg, M. R. 1992. Breeding patterns in a fringe population of fire salamanders, *Salamandra salamandra*. – *Herpetol. J.* 2: 54-58
- 1994. Population ecology, breeding activity, longevity and reproductive strategies of *Salamandra salamandra* during an 18-years long study of an isolated population on Mt. Carmel, Israel. – *Mertensiella* 4: 399-421